ANALYSIS

Vol. 21, Issue 67, 2020

ISSN 2319–5746 EISSN 2319–5754

Species

Pollination and fruit dispersal in the Fragrant Screw Pine, *Pandanus odorifer* (Forssk.) Kuntze (Pandanaceae)

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Article History
Received: 03 January 2020
Accepted: 19 February 2020
Published: February 2020

Citation
Solomon Raju AJ, Lakshminarayana G, Ch. Prasada Rao, Dileepu Kumar B, Santhi Kumari M, Prasad KBJ, Divyasree M, Suneetha Rani T. Pollination and fruit dispersal in the Fragrant Screw Pine, *Pandanus odorifer* (Forssk.) Kuntze (Pandanaceae). *Species*, 2020, 21(67), 113-119

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General Note
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ABSTRACT

Pandanus odorifer is a gregarious perennial evergreen dioecious tree species. It is typically a rainy season bloomer. Male inflorescences produce strong sweet fragrance while female inflorescences are totally scent-less. In both plants, the flowers are

minute, nectar-less and perianth-less; the male flowers represent only stamens while female flowers represent naked pistils which are aggregated into syncarps and each syncarp consists of several pistils but their carpels are fused and each carpel contains a single ovule. The plant is typically anemophilous. The plant also reproduces asexually through apomixis in the absence of pollination and by the offshoots of young plants that detach from the basal part of the trunk. In female plants, the syncarp consisting of several seeds produced from individual flowers is the unit of dispersal and it is hydrochorous. Seeds of a single syncarp germinate and produce either male or female or both plants. Therefore, the function of anemophily and apomixis in *P. odorifer* ensures it to populate itself, produce sexually breeding populations and colonize new areas. The study suggests that *P. odorifer* is a highly valued coastal species in the socio-economic fabric of the local communities and in the ecological integrity of shoreline.

Key words: *Pandanus odorifer*, dioecy, fragrantic male inflorescences, syncarp, polydrupe, anemophily, apomixis, hydrochory.

1. INTRODUCTION

Pandanus is a genus of Pandanaceae of monocotyledons. It contains around 600 species of trees and shrubs distributed from sea level to the highest peaks in the Old World tropics from East Africa westward through Indomalaysia to remote Island of Polynesia (Stone 1966; Kirtikar et al. 1991). In India, this genus has 30-40 species of this genus but they have not been well defined (Kirtikar et al. 1991). In Indonesia, many species of *Pandanus* are used for daily purposes as raw materials for mats and handicrafts such as hats and bags (Rahayu et al. 2007). *P. odorifer* is a dominant coastal species in South and Southeast Asia and effective in providing protection from tsunami damage due to its density and complex aerial root structure (Tanaka et al. 2007).

Watson and Dallwitz (1992) noted that the genus *Pandanus* is adapted for pollination mostly by wind and followed by insects, birds and bats. Cox (1985) reported that *P. tectorius* produces scent from the bracts of male inflorescences to attract pollinators but specific pollinators are not known. This author based on field experiments mentioned that the pollen is primarily carried to female flowers by wind. Cox (1990) documented that pollination biology of all *Pandanus* species is not studied. In this context, he worked on *P. tectorius* and reported that this species is specialized for anemophily and displays facultative apomixis which functions in the absence of pollination to produce viable seed.

In *Pandanus,* the fruit is buoyant and utilizes two separate dispersal mechanisms. The first is tidal water and ocean currents that disperse the buoyant fruits effectively. The second dispersal mechanism involves the fruit to use its colors to attract animals such as crabs, tortoises, lizards, cassowary, rats, and flying foxes for dispersal; these animals feed on the fleshy base of the fruit. These animals do not damage the seed contained within the fruit due to its hard bony endocarp which surrounds and protects the seeds (Ash 1987; Bennett 2000; Cox 1990; Gaulke 2010; Lee 1985; Wiles et al. 1991).

P. fascicularis is well distributed in South-East Asia and extended up to Papua New Guinea, North Australia and Pacific Islands (Panda et al. 2012). In India, it is a densely populated species distributed in the coastal regions of Odisha, Andhra Pradesh, Kerala, Tamil Nadu, Kerala and some regions of Uttar Pradesh and Gujarat (Chatterjee and Pakrashi 2001). Its leaves, fruits and male flowers are used in traditional medicine (Meilleur et al. 1997; Udupa et al. 2011; Adkar and Bhaskar 2014), as fence for protection from cattle due to possession of stiff and spines on the leaves, for making mats, ropes, baskets and purses and thatched house construction (Little and Skolmen 1989). The oil extracted from the distillation of male inflorescences is used for treating headache, rheumatoid arthritis, spasms and leprosy, valued in perfumery industry (Adkar and Bhaskar 2014) and as an effective sand binder (Aparna and Raja Sekhar 2015). Panda et al. (2007) reported that *P. fascicularis* growing in agricultural field effectively prevents soil erosion and growing along the sea shore stabilizes sand dunes reducing the impact of winds and thereby protecting the coastline. It is a highly valued coastal biological resource that contributes significantly to the socio-economy and ecology of the region. Despite its multiple uses in the socio-economy and ecology of the regions of its distribution, it has not been investigated for its pollination biology and fruit dispersal. Therefore, the present study has been contemplated to describe the pollination and fruit dispersal aspects of *P. odorifer* growing naturally in Bhavanapadu, a coastal village located in Srikakulam District of north coastal Andhra Pradesh, India. In this paper, *P. facicularis* Lam. is treated as synonym for *P. odorifer* (Forssk.) Kuntze according to the classification given in APG (2016) and described the details of the study accordingly.

2. MATERIALS AND METHODS

Pandanus odorifer (Forssk.) Kuntze (= P. *fascicularis* Lam) populations growing along beaches and margins at Bhavanapadu Mangrove habitat was selected for the present study during April 2018 to April 2019. This mangrove habitat is situated about 20 km from Tekkali in Srikakulam District of Andhra Pradesh State, India. This mangrove area is characterized by a few sparsely distributed

true mangrove plant species such as *Ceriops decandra, Bruguiera cylindrica, Sonneratia apetala, Avicennia marina* and profusely distributed mangrove associate plant species such as *Acanthus ilicifolius, Myriostachya wightiana, Sesuvium portulacastrum, Suaeda maritima, S. nodiflora* and *S. monoica*. Field visits were made at monthly intervals to record flowering season initially and then carry out details of pollination and fruit dispersal studies of *P. odorifer*. Field observations were made on male and female plants during flowering period to record details of inflorescences and flowers of each sex. The technical aspects of the inflorescences and flowers with reference to their functional traits to characterize pollination syndrome. Close-up observations were made on pollen dispersal from male plants by wind during daytime. The characters of stamens and anthers together with anther dehiscence time and pollen grain traits were also recorded. Female inflorescence was carefully examined to characterize cephalium and syncarps or phalanges during flowering phase and polydrupes during fruit formation, development and maturation phases. Further, syncarps were examined for internal details such as carpel fusion and seed production from several female flowers. Field observations were carefully made on the asexual modes of reproduction to record offshoot and apomictic modes. In the latter case, five female inflorescences which have not initiated flowering were bagged and followed for three months to record fruit and seed set. The syncarps produced in these inflorescences were cut and noted whether seeds were produced. Fruit (syncarps) dispersal aspects were also observed in the field to note the unit and mode of dispersal. The socio-economic and ecological values were noted by making enquiries with local people.

3. RESULTS

Pandanus odorifer is a small gregarious perennial evergreen tree with a flexuous trunk supported by brace roots (Figure 1a). It grows well and forms dense groves in damp areas with or without water-logged conditions along the coastal belts, riverbanks and canals. It is propagated mainly from seeds and also vegetatively by the offshoots of young plants that grow around the base of the trunk (Figure 1b). Leaves grow in clusters at the branch tips; they are fragrant, sword-shaped, stiff and bluish green consisting of spines at apex and below the midrib and margins. The plant is dioecious with separate male and female plants but their sex is identifiable only during their flowering season. The flowering occurs during July-October but extends up to January in some individuals occurring in highly water-saturated habitats.

In male plants, the inflorescence is terminal, pendulous, spadix with several subsessile cylindric spikes, each enclosed in long attractive white to yellowish green fragrant caudate-acuminate spathes which represent bracts as modified leaves. Each spike consists of numerous minute individually indistinguishable nectar-less flowers that consist only of stamens and totally lacking perianth parts. The stamens are laterally attached to stamenophores or directly to spadix; the latter situation is prominent at the apical part of spadix. The anthers are linear, longer than stamenophores, basifixed, dehisce by longitudinal slits and produce a copious amount of pollen. The pollen grains are sub-globose to ovoid, monocolpate monads lacking pollenkitt substance. The inter-node between spikes is elongated and enables swinging of the spikes due to which the light powdery pollen lacking pollenkitt substance blows easily by wind. The male flowers last only a single day.



Figure 1. *Pandanus odorifer:* a. Habitat, b. Left – Male inflorescence, Right - Vegetative phase, c. Fruiting phase, d. Close-up view of fruit.

In female plants, the inflorescence is a syncarpous pendulous globose or slightly cylindrical cephalium. Numerous papery pale yellow bracts are produced and inserted tristichously beneath the cephalium. The cephalium consists of 60-87 phalanges and each phalange is comprised of 4-11 small indistinguishable flowers. In each phalange, the carpels of all flowers are connate below but free above, yellow to orange to yellowish brown from base to apex. The flowers are nectar-less, lack perianth parts and have naked pistils. The ovary is unilocular with one basal ovule; the style is absent and the stigma is distinct and slightly protruded at the apex. The stigma receptivity begins as soon as the pistils are mature and continues until the initiation of fruit formation. The cephalium with tristichous arrangement of papery bracts facilitate the stigmas of all phalanges to capture pollen easily and efficiently.

The male inflorescences display flowers with dehisced anthers early in the morning and produce strong sweet fragrance. Female inflorescences also display flowers at the same time but the stigmas remain receptive until the initiation of fruit development in individual carpels. Male inflorescences offer pollen as pollinator reward while female inflorescences do not offer any reward to pollinators. Both male and female inflorescences were never visited by any insect species although the latter were present in the habitat indicating that the plant is not adapted for insect-pollination. The pollen shedding and dispersal occurred throughout the day by wind but its dispersal rate was found related to the prevailing wind speeds. With both male and female plants are located in the habitat, wind-blown pollen was found reaching the stigmas of female inflorescences. Further, inflorescences on female plants bagged for apomixis produced fruits with viable seeds indicating that the plant produces fruits even in the absence of pollination through asexual reproduction.

Fruits begin to mature as soon as the ovules are fertilized in the female cephalium (Figure 1c). The stigmas are persistent and appear as raised black or brown protrusions on the apex of the fruit. A fruit is a large indehiscent, pine-apple-shaped, syncarpous polydrupe formed from aggregated individual connate, angled and fibrous phalanges (Figure 1d). Each drupe is an aggregation and fused naked pistils in a phalange, brightly coloured and produces several seeds depending on the number of pistils or carpels present in the phalange; in effect, the drupe represents a multi-seeded fruit. The apical portion of the ripe drupe is woody, the upper mesocarp is hollow and traversed by fibers, the basal mesocarp is an orange-colored fibrous sweet flesh, and the endocarp is bony and positioned in the center of the carpel. The endocarp of the carpel contains a solitary minute, obovoid seed which is whitish inside and red-brown outside.

Individual drupes representing syncarpous fruits formed from phalanges consisting of several female flowers separate at maturity from the cephalium. The drupes or phalanges are buoyant and dispersed by water in tidal flats and by ocean currents. A single drupe with several seeds formed from several female flowers in a phalange dispersed by water and settled in a new water-saturated damp area has the chance to produce male and female plants and establish a new breeding population. Female plants form viable seeds if not pollinated by wind through apomixis and establish only a female population. In course of time, if a male-plant producing seed included in the drupe arrives or wind-blown pollen reaches the stigmas of this female population from the plants located far away, then the female population would initiate the establishment of a breeding population.

4. DISCUSSION

Pandanus fascicularis now treated as *P. odorifer* has been reported to flower during June-November in Visakhapatnam, Andhra Pradesh (Janaki Bai and Subba Reddi 1982). Later, this species has been reported to exhibit three flowering seasons in India, hot season (May-June), rainy season (July-September) and cool season (October-November) by Gurmeet and Amrita (2015). In the present study conducted in Visakhapatnam, found that *P. odorifer* is typically a rainy season bloomer but it extends flowering period in situations of water-saturated or water-logged habitats. It is a dioecious species with typical male and female flowers borne on different plants. But, it is practically impossible to identify the plant sex during vegetative growth as plants of both sexes appear morphologically similar. In the observed study region, *P. odorifer* has both male and female plants in the habitats of its occurrence indicating that they have the ability to breed sexually. Further, each sex individually propagates vegetatively by the offshoots that grow around the trunk base.

The genus *Pandanus* is primarily adapted for pollination by wind and followed by insects, birds and bats (Watson and Dallwitz 1992). In *P. tectorius*, male inflorescences produce scent to attract pollinators but specific pollinators are unknown. Experimental study on pollination indicated that this species is specialized for anemophily (Cox 1985; 1990). The plants in general use the scent produced by flowers as a bait for attracting insects for pollination and physiologically as a defense mechanism for protection against biotic and abiotic stresses. Further, the yield and composition of the metabolites that contribute to scent emission are influenced vastly by the environment in which the plants grow (Staudt and Bertin 1998; Gershenzon et al. 2000). In the present study, *P. odorifer* produces strong sweet fragrance only from male inflorescences, especially from spathes enclosing male spikes while female inflorescences are scentless. The flowers of both sexes do not secret nectar as they totally lack perianth; the stamens represent male

flowers while naked pistils represent female flowers. In the habitat of the plants, various insect species, especially bees such as honey bees, digger bees, leaf-cutter bees, carpenter bees and mason bees have been found but none of these bees or any other inspect species visited male and female inflorescences for pollen collection indicating that sweet fragrance is unable to attract them to male flowers. This finding is a deviation from the report by Cox (1990) that bees are frequent visitors to fragrance producing staminate inflorescences of *P. tectorius*; however, this author also noted that bees seldom visit pistillate inflorescences indicating that even if bees visit staminate inflorescences they are not qualified as pollinators because they are not attracted to scent-less pistillate inflorescences. Further, male and female flowers in this species do not produce nectar and only male flowers offer pollen as pollinator reward. The present study on *P. odorifer* indicates that fragrance production by male inflorescences appears to serve as a deterrent to prevent insect herbivores from feeding on pollen or bracts that enclose the male spikes. It is appropriate to mention the statement by Gressit (2012) that male flower bracts of *Pandanus* may be palatable to various insects. The scent-less female inflorescences lacking any floral reward have limited opportunities to be visited by pollinator insects, especially bees. Therefore, the scent production from male inflorescences appears to be primarily meant for discouraging insect herbivores that feed on pollen and bracts of male spikes.

Cox (1990) reported that *P. tectorius* is specialized for anemophily. The staminate inflorescences produce copious pollen devoid of pollenkitt which blows easily by wind. Further, paniculate inflorescences with elongated internodes are pendant and facilitate effective pollen dispersal by wind. The pollen thus dispersed is efficiently captured by pistillate inflorescences in which the female flowers with long period of stigma receptivity are specially covered by chartaceous bracts. In *P. odorifer*, the male spicate inflorescence with elongated internodes enabling them to be pendulous and dispersing pollen devoid of pollenkitt effectively by wind and female flowers with long period of stigma receptivity protected by tristichously arranged papery bracts enabling them to efficient capture pollen from the wind are perfect adaptations for anemophily. Further, anemophilous flowers do not require the production of pollinators rewards but they need to produce huge amount of pollen to ensure arrival of sufficient pollen on the receptive stigmas of female flowers. The male inflorescences consisting of several spikes and each spike consisting of numerous male flowers, and each anther producing copious amount of pollen substantiate that it is a highly evolved additional anemophilous trait. Therefore, *P. odorifer* is typically anemophilous.

Cox (1985; 1990) reported that *P. tectorius* is both anemophilous and apomictic indicating that it is facultative apomictic. It produces fruits through apomixis in the absence of anemophilous pollination. Similarly, in the present study, *P. odorifer* has also been found to produce fruits with viable seeds through apomixis as realized in the bagging experiment. This suggest that *P. odorifer* is also a facultative apomictic and apomixis as a means of asexual reproduction is a fail-safe strategy ensures this species to reproduce in the absence of pollination by wind.

The primary unit of dispersal in most *Pandanus* species is the brightly coloured syncarp (Cox 1990). In the coastal species, *P. tectorius*, the syncarps are buoyant (Gunn and Dennis 1976), dispersed primarily by ocean currents (Ridley 1930) and also by crabs (Lee 1985). In the freshwater species, *P. helicopus*, the syncarps are dispersed by turtles in Malay Peninsula (Stone 1982). In the present study, *P. odorifer* also uses the syncarp as a primary unit of dispersal and dispersed by tidal water characterizing the function of hydrochory. A single female inflorescence produces poly syncarps and each syncarp has many seeds produced from several connate flowers. The dispersal of a single syncarp means that the dispersal of several seeds as a single unit and germinate consequent upon the decomposition of woody apical part, mesocarp and endocarp. The seeds are most likely to germinate while in the decomposition phase of the syncarp. A single syncarp dispersed to a new habitat could establish a sexually reproductive population because, several seeds in each syncarp have chances to produce both male and female plants at the same time (Lee 1989). In case of production of only female plants from the dispersed syncarps in new areas, they produce only female plant population through apomixis and in course of time, if male seed or wind-blown pollen arrives at this population, then it subsequently establishes a sexually breeding population. Therefore, the function of anemophily and apomixis in *P. odorifer* ensures it to populate itself, produce sexually breeding populations and colonize new areas.

Fritts and Leasman-Tanner (2001) reported that *B. irregularis* was introduced to Guam where it often takes refuge in *Pandanus* trees and feeds on the insects, birds and lizards. It caused cascading ecological effects by removing native pollinators causing the subsequent decline of native plant species. Later, Hetherington et al. (2008) also reported that *Pandanus* trees are used as a refuge by a climbing brown tree snake, *Boisa irregularis* in Guam. Gurmeet and Amrita (2015) mentioned that Snakes co-habit near *Pandanus* plants due to their fragrance. The present study reports that *P. odorifer* habitat is used by snakes (not identified) and in one instance it was used by Indian Cobra, *Naja naja* as its refuge. But, we consider that the snakes are not attracted to *P. odorifer* just by the fragrance of male inflorescences. The snakes regularly use the special form leaf arrangement at the apical part of the shoot for shelter throughout the year irrespective of whether the plants are in flowering phase or not. Further, the snakes also take refuge in the female plants which do not produce any fragrance from their flowers. In general, they favor the water-logged or water-

saturated damp areas because they are the sources of frogs, toads and other food resources used by them. Therefore, *Pandanus* genus in general and *P. odorifer* in particular is a haven for snakes that inhabit coastal and inland wetlands.

Different authors reported that *P. odorifer* has socio-economic and ecological values. Its leaves, trunk, root and male inflorescences are used in various ways in the daily life of local communities. Of different plants, male inflorescences are highly valued and exploited as a very important source of perfume and in fact perfumery industries are flourishing in the areas of its distribution (Meilleur et al. 1997; Chatterjee and Pakrashi 2001; Udupa et al. 2011; Panda et al. 2012; Adkar and Bhaskar 2014). It is an effective sand binder, stabilizes shoreline and reduces high wind impacts protecting the coastline (Panda et al. 2007; Pattanaik et al. 2008; Aparna and Rajasekhar 2015). Field enquiries revealed that the male inflorescences, especially the floral bracts are traditionally used to impart the fragrance to clothes (Nadaf and Zanan 2013) and worn by women in their hair. Therefore, *P. odorifer* is a highly valued coastal species in the socio-economic fabric of the local communities and in the ecological integrity of shoreline.

5. CONCLUSION

Pandanus odorifer is a gregarious perennial evergreen dioecious tree species. It is typically a rainy season bloomer. The plant sex can be identified only during flowering season. During flowering, male plants produce strong sweet fragrance from their inflorescences especially from spathes that enclose male spikes. Female plants do not produce any fragrance from their inflorescences. In both plants, the flowers are minute, nectar-less and perianth-less; the male flowers represent only stamens while female flowers represent naked pistils which are aggregated into syncarps and each syncarp consists of several pistils but their carpels are fused and each carpel contains a single ovule. The male inflorescences with huge pollen lacking pollenkitt and female inflorescences with pistils enclosed by a common tristichously arranged bracts, and pendant orientation of both inflorescences are perfect adaptations for anemophily. Accordingly, the pollen dispersal from male to female plants occurs by wind. The fragrance produced by male inflorescences appears to be a fool-proof strategy to discourage insect herbivores from feeding on pollen and bracts. The plant also reproduces asexually through apomixis in the absence of pollination and by the offshoots of young plants that detach from the basal part of the trunk. In female plants, the syncarp consisting of several seeds produced from individual flowers is the unit of dispersal and it is hydrochorous. Seeds of a single syncarp germinate and produce either male or female or both plants. Therefore, the function of anemophily and apomixis in *P. odorifer* ensures it to populate itself, produce sexually breeding populations and colonize new areas. The study suggests that *P. odorifer* is a highly valued coastal species in the socio-economic fabric of the local communities and in the ecological integrity of shoreline.

Acknowledgement

All authors thank the Andhra University, Visakhapatnam, for providing physical facilities to carry out this research work.

Author's contributions

All authors contributed equally.

Funding: This study has not received any external funding.

Conflict of Interest: The authors declare that there are no conflicts of interests.

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